THE NAUTILOID CEPHALOPOD ORDER ACTINOCERIDA IN THE BRITISH SILURIAN

by CHARLES HEPWORTH HOLLAND

ABSTRACT. Five British Silurian species of the cephalopod order Actinocerida are described: one of *Ormoceras*, one of *Eldroceras*, and three of *Armenoceras*, including *A. cygneum* sp. nov. Their sparse distribution stratigraphically and geographically is reviewed. There are comments on the endosiphuncular vascular system.

OF the several thousand specimens of British Silurian cephalopods available for study only just more than 30 can be assigned to the order Actinocerida. They are not well preserved. Apical ends and body chambers are always missing. Preservation is largely in calcite or sandstone. In some cases little more than the siphuncle is seen, a situation common in other parts of the world. Most of the specimens are recorded from the upper Llandovery, but a few are found in Wenlock and Ludlow rocks. Almost all are from England and Wales.

Repository abbreviations. BGS: British Geological Survey, Keyworth; BMNH: The Natural History Museum, London; NMW: National Museums and Galleries of Wales, Cardiff; OUM: Oxford University Museum; RSM: Royal Scottish Museums, Edinburgh.

SYSTEMATIC PALAEONTOLOGY

Order ACTINOCERIDA Teichert, 1933
Family ORMOCERATIDAE Saemann, 1853

Genus ORMOCERAS Stokes, 1840

Ormoceras baccatum (Woodward, 1868)

Text-figure 2C, E

1868 *Actinoceras baccatum* Woodward, p. 133, pl. 8.
1888 *Actinoceras baccatum* Woodward; Foord, p. 174.
1982 *Actinoceras baccatum* Woodward; Phillips, p. 1.

Holotype. BMNH C9145 (Text-fig. 2E), Woolhope Limestone, Little Hope Quarry, near Woolhope, Herefordshire.

Paratype. OUM C198 (Text-fig. 2C), Woolhope Limestone, Woolhope.

Other material. BMNH C5250, Woolhope Limestone, Scutterdine (= Little Hope) Quarry, near Woolhope. BMNH C34050, Woolhope Limestone, locality confusingly given as ?Aymestry.

Diagnosis. Orthocone with rate of increase of *c.* 6–8°. Septa strongly concave with depth about 30 to 40 per cent. of diameter of shell. Cameral depth about 30 per cent. of diameter. Siphuncle sub-central, a little over one-third diameter of shell. Segments of siphuncle globular to slightly longer than wide or slightly wider than long. Endosiphuncular deposits with radial divisions and an equatorial division. Radial canals perpendicular to central canal.

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Description. The holotype shell is embedded in a block of Woolhope Limestone. The camerae are hollow or partly filled with calcite. These infillings are more prominent on the left hand side of the specimen. The maximum length seen is 93 mm. The septal necks cannot be distinguished. The layer of calcite which has been exfoliated to reveal the divisions of the endosiphuncular deposits appears to represent the perispatium and the connecting rings.

The paratype (Text-fig 2C), although in a similar block of limestone is preserved somewhat differently. The central canal and radial canals are clearly seen. At the apical end there are traces of the short-brimmed septal necks. The hollows, which represent the positions of the septa, give evidence also of hyposeptal deposits, increasing in size adapically.

Specimen BMNH C5250 is similar to the holotype but is poorly preserved. A length of 130 mm is seen. The rate of increase appears to be greater. The siphuncular segments are globular with a diameter of 8 mm. BMNH C34050 is a small, obliquely cut section showing part of the siphuncle, half in calcite and half infilled with fine sediment. There is some distortion but the segments are globular, measuring about 14 mm long and 15 mm wide.

Remarks. The siphuncular structure is typical of *Ormoceras*. Woodward began his description of the holotype (Text-fig. 2E) in the characteristic manner of the time: 'The fossil about to be described was obligingly sent to me by Dr. Bull, of Hereford, having been happily rescued from the remorseless hammer of the road-mender, by Richard Johnson, Esq., the Town Clerk of that city.' His plate 8 is a lithograph by Bull. The specimen is fractured with removal of the upper surface. Body chamber and apical end are both absent. Woodward referred to seven perfect and two fractured beads of the siphuncle. Two have been lost, perhaps accounting for Foord's (1888) description of the type specimen. Foord found the shell to be a little curved 'perhaps by distortion', and certainly the segments of the siphuncle suggest that this has occurred.

Family ARMENOCERATIDAE Troedsson, 1926

Genus ARMENOCERAS Foerste, 1924

Armenoceras nummularium (J. de C. Sowerby, *in* Murchison, 1839)

Plate 1, figures 1, 4–5; Text-figure 1A–C

1839 *Orthoceras nummularius* Sowerby, *in* Murchison, p. 632, pl. 13, fig. 24.
1872 *Actinoceras nummularium* (Sowerby); Salter, *in* Murchison, p. 534, pl. 26, fig. 5.
1882 *Orthoceras* (*Actinoceras*) *cochleatum* (Schlotheim); Blake, p. 61, pl. 15, ?fig. 8, *non* fig. 7,
1888 *Actinoceras nummularium?* Sowerby; Foord, p. 176.
1956 *Actinoceras nummularium* (J. de C. Sowerby); Curtis, p. 150.
1982 *Actinoceras nummularium* (J. de C. Sowerby); Phillips, p. 1.

Holotype. BMNH C3501 (Pl. 1, figs 1, 5), Wenlock, probably lower limestone or *Pycnactis* Band according to Curtis (1956), Whitfield Quarry, Tortworth, Gloucesteshire (Avon).

Paratype. BGS GSM 105055 (Text-fig. 1C), Upper Llandovery, Craig-yr-myddon.

EXPLANATION OF PLATE 1

Figs 1, 4–5. *Armenoceras nummularium* (J. de C. Sowerby, 1839). 1, 5, BMNH C3501 (holotype); Wenlock, Tortworth. 1, adoral view with marginal siphuncle; ×1. 5, lateral but slightly adoral view showing two camerae. 4, Bristol City Museum Cc831:6589; upper Llandovery, Tortworth; ×1·37.

Fig. 2. *Huronia vertebralis canadense* (Billings); Geological Survey of Canada, Ottawa, 2544 (holotype); Chicotte, South West Point, Anticosti, Canada; ×2.

Figs 3, 6. *Eldroceras blakei* (Foord, 1888). 3, OUM C24617; upper Llandovery, ?Malvern; ×2. 6, BMNH C48745 (holotype); probably Upper Llandovery, near Builth; ×0·6.

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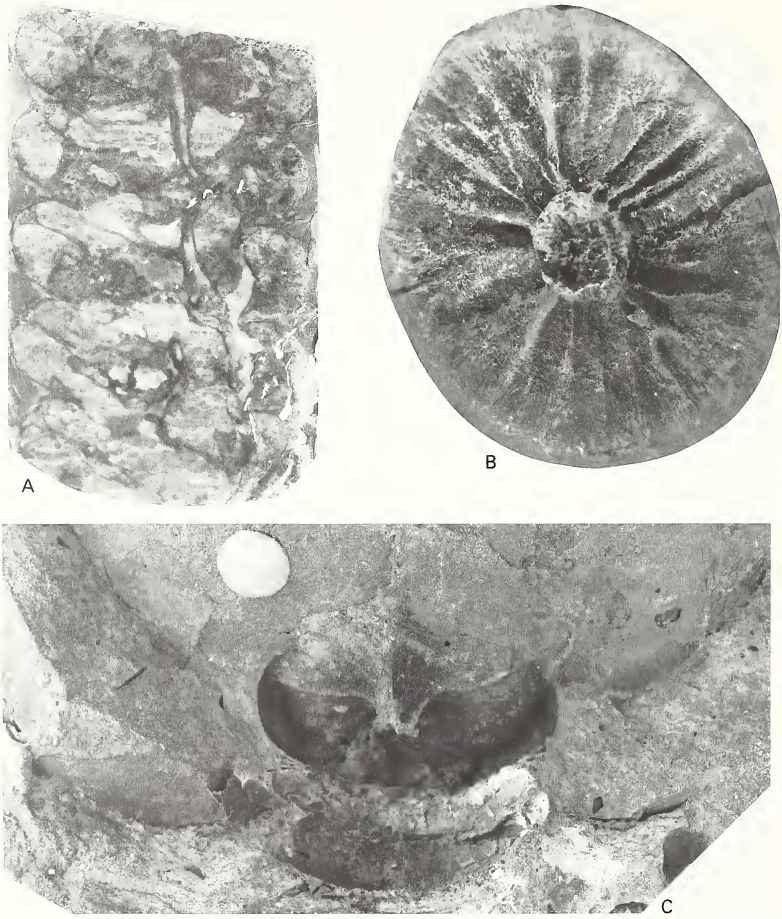
HOLLAND, *Armenoceras, Huronia, Eldroceras*



TEXT-FIG. 1. *Armenoceras nummularium* (J. de C. Sowerby, 1839). A, RSM 1885/26; Silurian, Pentland Hills; × 2. B, BGS RK 1887; Cae Eithin, Denbigh; × 3·4. C, BGS GSM 105055 (paratype); Upper Llandovery, Craig-yr-myddon; × 3.

Other material. BMNH C1980, Ludlow, Usk. BMNH C1989, upper Ludlow, Graigwith, Usk, Monmouth (Gwent). Bristol City Museum Ce831:6589 (Pl. 1, fig. 4), upper Llandovery, Damery Beds, ?*Palaeocyclus* band, Eastwood Park, Tortworth. BGS Geol. Soc. Coll. GSb 4517, Damery Beds, Long Quarry, Tortworth. BGS

RK 1887 (Text-fig. 1B), Central Electricity Generating Board pylon hole, Cae Eithin, Denbigh. Dudley Museum 12513, Wenlock, locality unknown. RSM 1885/26 (Text-fig. 1A), Pentland Hills.

Diagnosis. Relatively large orthocone with only slight rate of increase. Septal depth about 30 per cent. of diameter of shell. Cameral depth about 15 per cent. of diameter. Siphuncle sub-marginal. Rounded, disc-like segments inflated to about one-third diameter of shell, width about three to four times length. A system of radial endosiphuncular canals curves adorally from the central canal.

Description and remarks. The siphuncular structure is typical of *Armenoceras*. It is unfortunate that the holotype (Pl. 1, figs 1, 5) is an internal mould of only two camerae, although the position and shape of the siphuncle are clear. Diameter of conch seen is 75 mm. The paratype (BGS GSM 105055) is a similar mould, but, in addition to broken parts of three camerae, shows endosiphuncular canals and central tube (Text-fig. 1C). There is also an isolated mould of this system (BGS RK1887), so similar (Text-fig. 1B) that it can reasonably be regarded as belonging to the same species. Blake (1882, pl. 15, fig. 8) illustrated another such. I was able to section a fragmentary and broken specimen from the Pentland Hills (RSM 1885/26). The septa appear to be oblique, but there is internal distortion. However, the central canal and radial canals are well seen (Text-fig 1A), the latter expanding into the perispatium. Specimen BGS Geol. Soc. Coll. GSb 4517 is a typical column of isolated siphuncular segments, of which ten are preserved. Another type of preservation (Pl. 1, fig. 4) is seen in an external mould in the collections of Bristol City Museum (Cc831:6589). There are traces of possible hyposeptal and episeptal cameral deposits here.

Armenoceras subconicum (d'Orbigny, 1850)

Text-figure 2B, D

1839 *Orthoceras conicum* J. de C. Sowerby, *in* Murchison 1839, p. 642, pl. 21, fig. 21.
1850 *Orthoceratites subconicus* d'Orbigny, p. 2.
1882 *Orthoceras subconicum* (d'Orbigny); Blake, p. 150, pl. 12, fig. 9.
1888 *Actinoceras subconicum* (d'Orbigny); Foord, p. 175.
1956 *Actinoceras subconicum* (d'Orbigny); Curtis, p. 149.

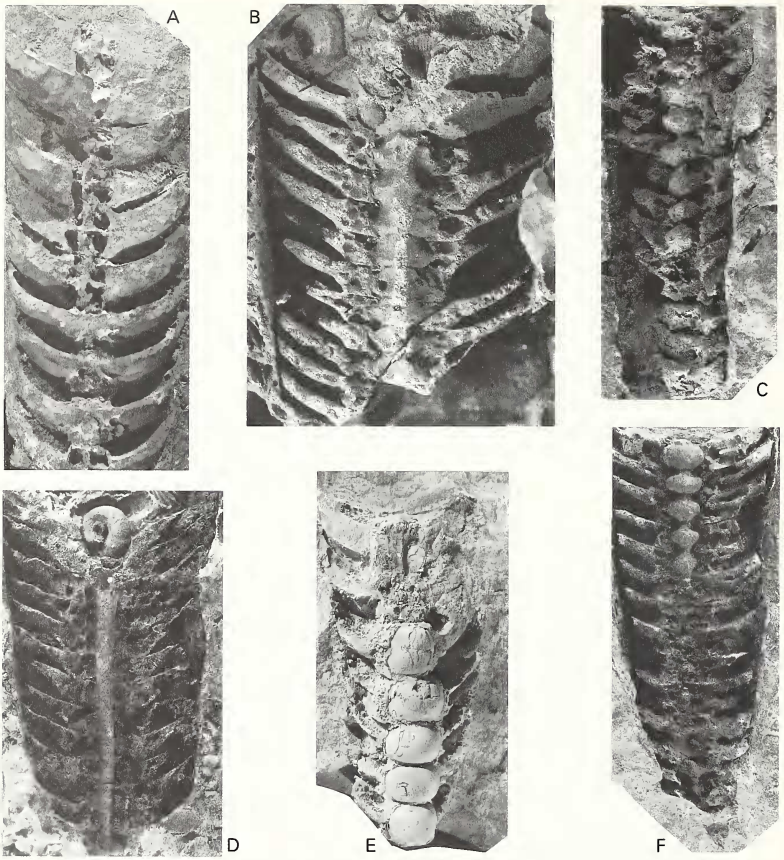
Holotype. BGS Geol. Soc. Coll. 6857 (Text-fig. 2B), upper Llandovery, Damery Beds, Michaelwood Chase, near Tortworth.

Other material. BGS GSM 105101, Wenlock Shale, Builth, Breconshire (Powys). BMNH C2032, upper Ludlow, Horeb Chapel, Monmouth (Gwent). Bristol City Museum Cc830:6589 (Text-fig. 2D), upper Llandovery, Damery Beds, Tortworth Inlier.

Diagnosis. Orthocone with rate of increase about 10°. Septa moderately concave with depth about 20 per cent. of diameter. Cameral depth about 17 per cent. of diameter. Siphuncle sub-central. Segments of siphuncle widely inflated to four or five times their length. Endosiphuncular deposits with complex lobation. Central canal prominent, cruciform to acutely triangular. Hyposeptal deposits present.

Description and remarks. As noted by Curtis (1956), the species was re-named by d'Orbigny (1850), when it was found that the name *Orthoceras conicum* was occupied (Hisinger 1837).

The siphuncular structure is typical of *Armenoceras*. The type specimen is preserved as an internal mould of chocolate brown rottenstone within a richly shelly band. The spongy appearance of the endosiphuncular area, on each side of the cruciform rod representing the central canal, testifies to a complex lobation of the endosiphuncular deposits. Sowerby's illustration gives an accurate impression of the holotype, but the associated shells are arranged differently from those on the specimen.



TEXT-FIG. 2. A, F, *Armenoceras cygneum* sp. nov.; upper Llandovery, Eastnor, Malvern. A, OUM C193 (paratype); ×2. F, OUM C192 (holotype); ×1·7. B, D, *Armenoceras subconicum* (d'Orbigny, 1850); upper Llandovery, Tortworth. B, BGS Geol. Soc. Coll. 6857 (holotype); ×2. D, Bristol City Museum Cc380·6859; ×1·4. C, E, *Ormoceras baccatum* (Woodward, 1868); Woolhope Limestone, Woolhope. C, OUM C198 (paratype); ×0·9. E, BMNH C9145 (holotype); ×0·6.

Specimen Cc830 is similar to the holotype in preservation and appearance, although the rod representing the central canal is acutely triangular.

Armenoceras cygneum sp. nov.

Text-figure 2A, F

Holotype. OUM C192 (Text-fig. 2F), upper Llandovery, Obelisk, Eastnor, Malvern.

Paratype. OUM C193 (Text-fig. 2A), as above.

Other material. BMNH C2003, upper Ludlow, Llanfrechfa, Usk, Monmouth (Gwent). BGS GSM 105051, Silurian, Marloes Bay, Pembrokeshire (Dyfed). BGS GSM 105258, upper Ludlow, Llanfrechfa. ?BGS GSM 105054, Silurian, Marloes Bay. ?Sedgwick Museum A.39547, Upper Llandovery, Three Chimneys, Marloes Bay.

Diagnosis. Relatively small orthocone with rate of increase of *c*. 6–10°. Septa relatively shallow with depth about 17 per cent. of diameter of shell. Cameral depth about 15 per cent. of diameter. Siphuncle sub-central. Segments of siphuncle inflated to about four times their length. Endosiphuncular deposits with complex lobation. Central canal expanded in adoral segments to globular or pear-shaped forms connected by slender necks. Hyposeptal deposits present.

Remarks. This form superficially resembles *A. subconicum* and is preserved as similar moulds; specimens have previously been identified as this species. The septa are less concave, but the striking difference is the peculiar form of the mould of the central canal. Teichert (1935) described as the 'pseudocone' the space left free between the endosiphuncular deposits in the upper part of the siphuncle. In the present species the deposits as so far developed in the adorally situated segments must have been so shaped as to leave globular to pear-shaped spaces in sequence between them.

Genus ELDROCERAS Foerste, 1924

Remarks. Foerste separated *Eldroceras* from *Armenoceras* on the basis of its being slightly curved apically. The segments of the siphuncle were described as 'presenting moderately convex vertical outlines; general form barrel shaped, the end flat, and in contact with the intervening part of the septa'. Teichert (1964) referred to the siphuncle as narrower than in *Armenoceras*, but still wider than long. The type species, *E. indianense*, has very distinctively barrel-shaped segments of the endosiphuncular deposits, with radial divisions and also an equatorial marking on the outside. Other illustrations by Foerste and in the *Treatise* show somewhat wider segments, but of similar outline. Subsequent attributions to the genus have tended to neglect the requirement of a curved apical end, which, since it is rarely seen to be present, is probably wise.

Eldroceras blakei (Foord, 1888)

Plate 1, figures 3, 6

1882 *Orthoceras* (*Actinoceras*) *cochleatum* Blake, p. 161, pl. 15, fig. 7, ?*non* fig. 8
1888 *Actinoceras Blakei* sp. nov., Foord p. 176.
1982 *Actinoceras blakei* Foord; Phillips, p. 1.

Holotype. BMNH C48745 (Pl. 1, fig. 6), probably upper Llandovery, Gwernyfed, near Builth, Breconshire (Powys).

Other material. BMNH C7506, Much Wenlock Limestone, Ledbury, Herefordshire. Ludlow Museum 05308, Ludlow, Gorstian Stage, upper Bringewood Formation, Leinthall Earls, Shropshire. NMW 13.140 G26, Wenlock, Deadman's Bay, Pembrokeshire. OUM C24617 (Pl. 1, fig. 3), upper Llandovery, ?Malvern. C29358, Upper Llandovery, Malvern.

Diagnosis. Orthocone with low rate of increase. Septa strongly concave. Cameral depth about 25 per cent. of diameter. Siphuncle sub-central. Endosiphuncular deposits with shape as for genus, their width less than twice their length. Radial divisions.

Description and remarks. Foord (1888) noted that 'Through an oversight, only a portion of the specimen in the British Museum was figured by Prof. Blake, but the remainder adds very little to our information respecting the species'. The illustration (Blake 1882, pl. 15, fig. 7), which is slightly imaginative, shows 7 siphuncular segments but, in addition, traces of the external mould of the surrounding shell and a few camerae below. The actual specimen (Pl. 1, fig. 6) has ten segments and part of another one adorally. There are slight traces of septa on one side. A maximum length of the siphuncle seen is about 140 mm. The connecting rings are missing. The endosiphuncular segments are clearly somewhat moved and distorted. Their maximum width is slightly above their equator. Radial markings are 1–2 mm apart. As Foerste stated in his description of the genus, their ends are flat where in contact with the intervening part of the septa (see, for example, Foerste and Teichert 1930, pl. 47, fig. 1). This particular feature is seen also in NMW 13.140 G26. Although the specimen is not well preserved and is distorted, it also shows hyposeptal deposits.

The collection in The Natural History Museum also contains a loose fragment which has broken from the remainder. The opportunity was taken to section this transversely and longitudinally. The transverse section shows the central canal and parts of three radial canals, one of which branches. A longitudinal view shows a radial canal approximately perpendicular to the axis of the siphuncle.

The other specimen in The Natural History Museum (BMNH C7506) shows only siphuncular segments of appropriate shape, 4–5 mm long and 6 mm wide. Proportions are similar in a Gorstian specimen in Ludlow Museum (05308), where the segments are 6×8 mm to 8×12 mm. Radial lines are present.

OUM C24617 is a smaller internal mould in sandstone (Pl. 1, fig. 3), with rate of increase of *c.* 4°. The maximum length seen is only 25 mm. Septal depth is 24 per cent. of diameter. Cameral depth 18 per cent. of diameter. The siphuncular segments measure 2·5 mm long by 3·5 mm wide. One shows faint radial lines. Although so much smaller than the other examples, this older specimen has all the same characteristics.

DISTRIBUTION

Of the relatively rare actinocerids described above, only *Ormoceras baccatum* does not extend in range from Upper Llandovery to Ludlow. It is confined to the Woolhope Limestone, a basal Wenlock facies restricted in geographical distribution. *Armenoceras nummularium*, *A. subconicum* and *Eldoceras blakei* are recorded from Wales and the Welsh Borderland, except for the single record of the first from Scotland. The new species, *A. cygneum*, is from the upper Llandovery of the Malverns and the upper Ludlow of Monmouth. Although such ranges are long, they are to be found also in some members of other Silurian groups. Most of the occurrences are from relatively shallow water carbonates or sandy clastics.

Irish Siliurian cephalopod faunas as a whole are very sparse. They have been reviewed recently by Evans (1994). He had one actinocerid taxon, represented by three fragments, probably all from the same individual, from the Wenlock of the Dingle peninsula, County Kerry. He identified this as *Eushantungoceras* aff. *pseudoimbricatum* (Barrande). Teichert (1964) regarded the genus *Eushantungoceras* as a synonymn of *Armenoceras*, a view with which I have sympathy. Its distinguishing characters are stated to be a very broad siphuncle, with a dorsally situated endosiphonal canal, and the massive development of endosiphuncular deposits ventrally. The specimens from Ireland are very similar, even to the extent of the relative width of the siphuncle, to *Armenoceras subconicum*. They are preserved in a similar way. However, the endosiphuncular canal of the latter is not marginal.

The genera *Armenoceras* and *Ormoceras* were cosmopolitan. *Eldroceras* was established in North America; its European occurrences are still to become more widely recognized. The most striking feature of Silurian actinocerid distribution is the North American arctic or circumpolar fauna of the

Llandovery, which later became replaced by more familiar European types. The genera *Huronia* and *Huroniella*, with the characteristic profiles of their siphuncular segments (usually found alone), are typical of the arctic fauna. For comparison, an example from Canada is illustrated in Plate 1, figure 2.

THE ENDOSIPHUNCULAR VASCULAR SYSTEM

Cameral deposits in orthoconic nautiloids are now generally accepted as of primary origin, difficult though it may be sometimes to distinguish them from secondary infillings. Flower (Flower 1957; Hook and Flower 1977) provided a charming illustration of the way their distribution in the individual shell served happily to bring it into an approximately horizontal attitude in the water. The cameral vascular system (cameral mantle of Flower), which secreted these deposits, was demonstrated in North American Silurian dolomitic internal cameral moulds of *Leurocycloceras* (Flower 1941) and in my own material of the same genus from the Ludlow rocks of Central Wales (Holland 1965).

The endosiphuncular deposits of the actinocerids, also, are regarded as weighting devices. Remarkable reconstructions of the complex system of central canal, radial tubes, and perispatium, which must all relate to the endosiphuncular vascular system, were first published by Teichert (1933) in his long German paper on the actincocerids. They appeared again in his shorter English version of the work (Teichert 1935) and in the relevant chapter of the *Treatise* (Teichert 1964, figs 133–134). The German paper shows the sectioned material upon which they are based and there are various other pertinent illustrations. Foerste (1924, pl. 2, fig. 3) and Foerste and Teichert (1930, pl. 47, fig. 2) are two examples.

The limited amount of British material described in the present paper provides its own evidence in the form of the radial and transverse markings, seen on the outside of the endosiphunular deposits when the connecting ring has gone (Pl. 1, fig. 6; Text-fig. 2E). The subdivision of the deposits so revealed must correspond to the arrangement of the vascular system, with its main branches forming perpendicular or curving radial tubes. There is evidence of the tubes themselves in *O. baccatum* (Text-fig 2C), and in fragmentary sectioned material of *A. nummularium* from the Pentland Hills (Text-fig. 1A).

The taxonomic usefulness of the configuration of the building blocks which make up the segments of the endosiphuncular deposits is limited by the varied degree of their preservation. Wade (1977) illustrated a remarkably complex configuration characterizing a new Ordovician family, Georginidae, from the Ordovician of Australia. Teichert and Crick (1974) illustrated a coral-like arrangement of radial lamellae in the siphuncle of *Huronia vertebralis* from the Silurian of Michigan. The British material shows a relatively simple arrangement in *Ormoceras*, of radial tubes perpendicular to the central canal. The evidence from *Armenoceras* is of tubes which curve adorally from the central canal before running outwards to a division at the perispatium.

There remains the question as to why these elaborate systems ever developed. The answer, I think, is that the relatively large siphuncles of the actinocerids demanded a compensating weighting device, just as did the camerae. The vascular system to provide this must have been constructed to allow passage also from the central canal out through the connecting ring into the camerae.

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